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1   Mate-choice copying accelerates species range expansion

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Abstract

Mate-choice copying is a type of social learning in which females can change their mate preference after observing the choice of others. This behaviour can potentially affect population evolution and ecology, namely through increased dispersal and reduced local adaptation. Here, we simulated the effects of mate-choice copying in populations expanding across an environmental gradient to understand whether it can accelerate or retard the expansion process. Two mate-choice copying strategies were used: when females target a single individual, and when females target similar individuals. We also simulated cases where the male trait singled out by females with mate-choice maps perfectly onto his genotype or is influenced by genotype-by-environment interactions. These rules have different effects on the results. When a trait is determined by genotype alone, populations where copier females target all similar males expand faster and the number of potential copiers increased. However, when preference is determined by genotype-by-environment interactions, populations where copier females target a single male had higher dispersal and also expand faster, but the potential number of copiers decreases. The results show that mate-choice copying can accelerate the expansion process, although its adaptiveness depends on the information animals' use in different contexts.

Introduction

Choosing a mate is one of the most important decisions an individual will make in his or her lifetime. If the choice is a maladaptive mate, there is a risk of having maladaptive offspring that may be eliminated from the population. Individuals can choose mates based on their innate preferences, or by learning from the choices of others [1]. The latter behaviour, known as mate-choice copying [2], is a type of social learning that has been found in numerous species across different taxa [3,4].

Many theoretical studies have attempted to understand how mate-choice copying can affect the evolution of secondary sexual traits in males [5,6] and the evolution of copying behaviour in females [7,8]. Because mate-choice copying can lead females to make choices that differ from their innate preferences, it has the potential to alter the

course of sexual selection in a population, which has attracted considerable interest from evolutionary biologists [9–16]. However, a detailed analysis of the role of this behaviour in large-scale ecological and evolutionary processes is still in its infancy.

Varela et al. [17] suggest that mate-choice copying should lead to convergence of mate preferences and reduced genetic differences between heterogeneous patches, as animals can share their preferences when dispersing. This was confirmed by Sapage et al. [18], who also found that copying promotes the evolution of dispersal because by copying local mate preferences individuals tend to produce offspring that are better adapted to the new patch, thus reducing dispersal costs. However, a side effect is an overall reduction in local adaptation due to the increased rates of gene flow between patches. These two effects raise an interesting question not addressed by Sapage et al. [18]: what is the role of mate-choice copying during range expansions? Does it accelerate or retard the expansion process?

Because in expanding populations the first individuals to arrive at a new habitat would likely be the ancestors of future generations, the expectation is that by promoting dispersal mate-choice copying can also accelerate the expansion process into new territories even if it is a neutral (or even slightly deleterious, e.g., [10]) behaviour, i.e., a phenomenon akin to gene surfing [19]. On the other hand, it is well known that the range of species is usually restricted due to negative growth rates of populations outside their preferred range, either because of high fragmentation at the edge of the range, or because of the inability of populations to adapt locally, thus producing maladapted individuals at the egde of the range [20]. Sexual selection, by inducing niche shifts at the range edge, can enhance the adaptation process, and facilitate population expansion [21]. However, mate-choice copying, being a behaviour that reduces local adaptation [18], can counteract the facilitating effect of sexual selection and ultimately reduce the rate of population expansion.

To understand whether mate-choice copying can speed up or slow down the ability of populations to expand into new territories, it is important to consider different types of mate-choice copying and of female preference rules.

Mate choice copying can occur when individuals learn to prefer specific mates (individual copying) or when they generalize the traits of model individuals to the entire population (generalized copying or trait-copying) [22]. Generalization is thought to have

99   stronger evolutionary consequences for evolution because copied preferences spread

100   more rapidly through in the population, whereas individual copying may affect only a few

101   individuals [4,23]. In other words, individual copying follows the "choose the exact same

102   male as demonstrator females" rule, leading females to mate with the same, "most popular"

103   male; whereas generalized copying follows the "choosing a similar enough male as

104   demonstrator females" rule, leading females to mate with different "similar enough"

105   males. This "similar enough" rule should be particularly important during dispersal as it

106   allows for individuals to assess mate quality in a new environment by learning from the

107   choice of conspecifics, rather than focusing on a single mate that might not be available.

108   Females may prefer different types of information about sexual traits [24], namely

109   information that is condition independent (e.g. orange area in male guppies, [25]), or

110   information based on genotype-by-environment interactions, which is condition

111   dependent (e.g., brightness of orange colour in male guppies, [25]). In the latter case,

112   condition is defined as the energy that an individual has available to allocate to the

113   expression of that trait [26], which, in turn, depends on the individual's ability to find

114   food and metabolize it. Some males, arriving in a new patch of habitat after dispersal,

115   may not be able to find sufficient resources or in sufficient quantities to allocate to their

116   ornaments or to maintain a good general condition. Therefore, females using condition-

117   dependent traits to assess the phenotypic quality of a given male can obtain information

118   about his ability to survive in a given habitat [27].

119   In this study, we use individual-based simulations to analyse the effects of these

120   different types of mate-choice copying and preference rules on the rate of population

121   expansion into a new, empty habitat. Given that mate-choice copying promotes dispersal

122   and reduces local adaptation [17,18], we predict that, when preference is for condition-

123   independent traits, copying should help individuals reach the edge of the population's

124   range, but then hinder their ability to invade a new patch, compared to a population

125   without copying. We further predict that this effect should be stronger with individual

126   copying, because to many females will choose the most popular males, who may be

127   maladapted to their new environment, further limiting the ability of the population to

128   adapt to new patches. Finally, we predict that the effect of copying on delaying range

129   expansion should be lower when female preference is condition dependent, because

130   females are able to directly assess the quality of their mates.

Material and methods

The models were adapted from Sapage et al. [18], with some dispersal concepts taken from Phillips [28]. We considered six polygynous population scenarios, crossing the type of copying strategy with the type of preference rule. For mate-choice copying types, females can show either (1) no copying, (2) individual copying, or (3) generalized copying. For preference rules, females can choose males based on either (1) a trait directly related to their genotype (condition independent on the environment), or (2) a performance trait resulting from genotype-by-environment interactions (condition dependent). We summarized all the relevant parameters and variables of the model in Table S1 in the Electronic supplementary material.

The simulated world is represented by a matrix with $y = 20$ rows and $x = 50$ columns, continuous in the y but not in the x axis (i.e., a cylinder, where the y-axis wraps around but the x-axis has edges). Dispersal can happen in any direction along the y-axis (up and down) and the x-axis (forward and backward). Columns (x-axis) are subdivided into three habitats: the original habitat as the 10 left-most columns with the starting distribution of the population (X_s), the environmental gradient defined by the next 30 columns (X_g), and the endmost habitat located at the final 10 columns (X_f). X_g and X_f have empty patches before the population starts expanding. The invasion front in X_g and X_f is defined by the furthest occupied patch in the x-axis, with the invasion front progressing along the cylinder. Each patch within each habitat has an environmental value e_{ij} $(i = 1, \cdots, Y; j = 1, \cdots, X)$ sampled from a normal distribution with mean $\overline{e_j} = 0.9$ in X_s and $\overline{e_j} = 0.1$ in X_f and standard deviation 0.01. In the environmental gradient X_g, $\overline{e_j}$ decreases linearly from 0.9 to 0.1 (Figure S1). The y-axis has, therefore, a small random noise component affecting the environment, and this random noise is different in each simulation run.

We model an obligately sexual, haploid population with five independent loci, some with sex-limited expression. **S** (for sex) determines whether individuals are female (0) or male (1). **T** (for trait) takes real values between 0 and 1 and defines the viability of the individual relative to the environmental value (see below). **T** has a pleiotropic effect in males, and codes for an observable phenotype that influences female choice. **P** (for

162   preference), expressed only by females, takes real values between 0 and 1 and codes for

163   the female preference relative to the male trait. **C** (for copy) is only expressed in females

164   of populations with copying and has two alleles that code for the ability of females to

165   mate-choice copy (*C*) or not (*c*). The copying behaviour did not involve direct costs in

166   the models. Finally, the **D** locus codes for the probability of individuals to disperse to

167   nearby patches and can take real values between 0 and 1. Note that **T** is the only locus

168   affecting fitness.

169   Initially, all patches in the initial habitat (the 10 left-most columns with 20 rows

170   each, $X_s = 20 \times 10 = 200$ patches) are at carrying capacity $K = 64$ individuals, each

171   with an equal probability of being female or male. This value of K was used because we

172   wanted patches with a large carrying capacity, so that enough individuals could invade

173   the environmental gradient, but not too large to avoid computational limitations.

174   Generations are discrete and nonoverlapping, so copying occurs within each generation.

175   In other words, we assume that mate-choice copying occurs through horizontal cultural

176   transmission as documented in several species [29 and references therein]. The order of

177   events is mate choice, followed by offspring production, then viability selection, and

178   finally dispersal. The sequence of four events represents one generation. Note that in our

179   model we assume that juveniles are selected in their natal environment before dispersing

180   to another patch to mate and reproduce. We made this assumption because individuals

181   can only breed for one season before dying (see below), so focusing on sexual selection

182   in the new patch can help to highlight the potential effects of mate-choice copying.

183   All initial individuals carry allele *c* (i.e., females are non-copying), have allelic **D**

184   values set to 0.02, and are locally adapted, i.e., their allelic **T** values were sampled from

185   a normal distribution centred on the environmental value of their patch $\overline{e_j} = 0.9$ with

186   standard deviation 0.01. For condition-independent populations, **P** allelic values were

187   sampled from the same distribution as the **T** allele values, whereas for condition-

188   dependent populations, **P** allelic values remained equal to 0 because female preference

189   depends on how well a male is adapted to their local environment during mate-choice

190   (see below). These values correspond the assumption that, at the start of the simulation,

191   females have an optimal preference to the most adapted males in their original patch, even

192   when preference is for condition-independent traits, whereas when preference is for

193   condition-dependent traits females have an optimal preference for the most adapted males

194   overall. Loci **T**, **D** and **P** (when preference is towards condition-independent traits) have

195 a mutation probability of 0.01. Once a mutation occurs, we add a normal random variable

196 of mean zero and standard deviation 0.02, keeping the allelic value in the interval $[0,1]$.

197 The **C** locus has a 0.005 probability of switching from c to C and vice versa. Note that

198 under this assumption the mutational equilibrium value for the copying allele C would be

199 0.5.

200   The expansion starts after a warmup phase of 2,500 generations to reach a stable

201 state before expansion, allowing for **T**, **P** and **D** to evolve naturally. Provided there is at

202 least one female and one male in a patch, females can choose based on their own innate

203 preference (non-copier) or perform copying (copier). Females with the C allele can

204 become non-copiers if and only if there are no females with the c allele within the patch

205 to copy from. Non-copier females assign a preference value towards a condition-

206 independent trait by scoring the males using

$$\phi_{\mathrm{Pref}}(f,m) = e^{-S_S(a_{Pf}-a_{Tm})^2}, \tag{1}$$

207

208 where S_S is the strength of sexual selection (choosiness), a_{Pf} is the allelic value for

209 preference, and a_{Tm} is male's trait value. In cases where females assign a preference

210 towards a condition-dependent trait, the score of the male is related to the difference

211 between the trait of the male and the environmental value, translating into

$$\phi_{\mathrm{Pref}}(f,m) = e^{-S_S(a_{Pf}-|a_{Tm}-e_{ij}|)^2}. \tag{2}$$

212

213 This expression shows why we set the allelic value for preference to 0 under condition-

214 dependent preference. Whenever the score is below 10^{-300} (a rare event), females ignore

215 the male.

216   Copier females choose after non-copier females, and we assume that can observe

217 all matings in a patch. In the case of individual copying, females count the number of

218 times each male has been chosen and mate with the most popular male (if there is a tie

219 they choose randomly among the popular males). In generalized copying, females assign

220 a social score to each male. Since the allelic values a_{Tm} are continuous in the interval

221 $[0,1]$ the social score depends not only on the popularity of the male but also on the

222 popularity of similar males. The social score for male m is

$$\phi_{\mathrm{Soc}}(m) = \sum_{m^*=1}^{M_{ij}} n_{m^*} e^{-S_S(a_{Tm}-a_{Tm^*})^2}, \tag{3}$$

223

224 where M_{ij} is the number of males in the patch and n_{m^*} is the number of times male m^*,

225 with allelic value a_{Tm^*}, is chosen by non-copier females. Considering m^{**} to be the most

226 popular male (i.e., the male with the highest social score in each patch), copier females

227 replace their own a_{Pf} value with the male's m^{**} allelic value $a_{Tm^{**}}$ in equation 1 if

228 preference is for condition-independent traits, or with $|a_{Tm^{**}} - e_{ij}|$ in equation 2 for

229 condition-dependent traits. This means that when the copier females choose based on

230 condition-dependent traits, they will tend to choose adapted males when they observe

231 other females choosing adapted males, and they will choose maladapted males when they

232 observe other females choosing maladapted males.

233   The expected number of offspring produced by each female is drawn from a

234 Poisson distribution with mean $\lambda = 4$. The offspring inherits a random copy of the

235 parental alleles. Survival probability depends on the survival score

$$\phi_{\text{Surv}}(n) = e^{-S_N(a_{Tm} - e_{ij})^2}, \qquad (4)$$

237 where $S_N = 500$ is the strength of viability selection. Individuals with the highest

238 survival score in each patch survive. The number of surviving individuals per patch is

239 calculated as the sum of its $\phi_{\text{Surv}}(n)$, with K as a hard upper bound. We used a relatively

240 high strength of viability selection so that populations can only expand successfully if

241 individuals in the invasion front can produce offspring with traits reasonably adapted to

242 their natal patch. Under these conditions, the rate of expansion is related to the ability of

243 populations to adapt their trait alleles to the new environment, although further adaptation

244 to the patch is theoretically still possible.

245   After passing the viability selection process, individuals can disperse to any of the

246 neighbouring patches with equal probability, controlled by the allelic values at locus **D**.

247 During dispersal, individuals have a 0.05 probability of dying, i.e. the risk of dispersal.

248 Here we implement a hard selection model where the contribution of a patch to the

249 migrant pool depends on the fitness of its individuals [30].

250   The simulation ends 1,000 generations after the endmost habitat is occupied at

251 80% carrying capacity, i.e. after the population is likely to have adapted to the new

252 environment. For each simulated run, we extracted the environmental matrix and, for each

253 column in each generation, the average allelic values and the position of the invasion front.

254 This allowed us to measure the number of generations taken for these populations to

breach the environmental gradient. By breach we mean the time it took for them to migrate from the initial habitat to the endmost habitat, having to go through a continuous adaptation phase across the environmental gradient [as in 28].

As are many parameters involved, we have explored the effects of some of the parameters that we considered the most relevant. We simulated different values of increasing choosiness for the six population types by setting S_S to 100, 500, and 1000. We also ran simulations with $S_S = 0$, where females choose randomly. With this parameter, populations with no copying and with generalized copying are conceptually identical, so we ran one set of simulations for both, allowing preference to evolve neutrally. To investigate the effects of dispersal on the invasion process, we additionally repeated all the simulations, but without allowing dispersal to evolve by setting **D** to an allelic value equal to 0.02 (close to the average value for most populations) and its mutation rate to 0. For each population type, we ran each parameter set 20 times.

The code is written in the C programming language with some functions from the GNU scientific library 2.3 (GSL) [31] and can be found in [32]. All data were analysed using the R software, version 4.1.1 [33].

Results

Case 1: Preference is condition independent

When females have a condition-independent preference towards the male trait and dispersal is allowed to evolve, populations with generalized copying breached the environmental gradient faster than populations with individual copying and populations without copying when $S_S > 0$ (Figure 1A and Table S2). However, the average dispersal allelic value after warmup, but before expansion, was around three times higher in populations with individual copying than in the other populations, even if non-copiers choose randomly (i.e., $S_S = 0$) (Figure 1B and Table S3).

In the simulations where dispersal is fixed, all populations take more generations to breach the environmental gradient (cf. Figures 1A and 1C). When choosiness (S_S) was high, individual copying also took more time to breach than the other populations whereas generalized copying took less time than the others (Figure 1C and Table S4).

The proportion of individuals with the *C* allele after warmup but before expansion in the population with generalized copying, was higher than the expected mutational equilibrium value of 0.5, particularly with higher choosiness whereas it was lower than 0.5 in populations with individual copying (Figure 1D and Table S5), even when non-copier females chose randomly.

To understand the distribution of copiers along the environment, we checked the proportion of individuals with the *C* allele per column (*x* coordinate) at the generation when the population breached the environmental gradient. Ignoring the large variation in the last few columns due to the extremely small number of individuals just at the invasion front, we found that the number of individuals with the *C* allele increased to about 0.95 near the invasion front in populations with generalized copying and decreased to about 0.05 in populations with individual copying (Figure 1E and Table S6). This result already suggests that generalized and individual copying play opposing roles during the invasion of new habitats.

Using the same approach, we checked if populations were adapting their innate preference during expansion by analysing the mismatch between the average preference allele and the expected environmental value ($\bar{e_j}$) for each column (*x* coordinate) during the generation where the populations breached the environmental gradient. Results show that populations with generalized copying have the tendency to make the preference allele adapt much less to new environments (Figure 1F).

Case 2: Preference is condition dependent

We ran the same set of simulations as above considering preference to be condition dependent, excluding the scenario where non-copier female choice is random ($S_S = 0$) because the simulations would be identical with the ones above. We did not analyse the adaptiveness of the preference allele, given that female innate preference is already towards the most adapted male trait in each patch.

With this preference rule, all populations breach the environmental gradient faster than when the preference is condition independent (cf. Figures 1A and 2A, and Table S2), and the effect is more evident with increasing choosiness. In high contrast with the case of condition-independent preference, we found that populations with individual copying

breached the environmental gradient much faster than the other populations (Figure 2A and Table S2).

Consistent with the observations for condition-independent preference, populations with individual copying showed a higher dispersal tendency than the other populations just prior to the population expansion (cf. Figures 1B and 2B, and Table S3). Simulations with fixed dispersal show no difference in breaching time between all populations, confirming dispersal to be a determinant factor for the increase in expansion speed for individual copying populations when preference is condition dependent (cf. Figures 1C and 2C, and Table S4).

When analysing the evolution of the copier allele after warmup but before expansion, populations with individual copying showed a slightly lower proportion of individuals with the C allele than in populations with generalized copying, similar to with the condition-independent scenario (cf. Figures 1D and 2D, and Table S5). The proportion of individuals with the C allele is not affected by choosiness (Figure 2D).

Looking at the proportion of individuals with the C allele per column (x coordinate) at the generation when the population breached the environmental gradient, we found that, when female preference is condition dependent, generalized copying decreases in the invasion front when choosiness is high ($S_S \geq 500$), in contrast to what we found with condition-independent preference (cf. Figure 1E and 2E).

Discussion

Mate-choice copying has the potential to affect speciation [9,10,13,16,17] and hybridization [17], as well as dispersal and local adaptation [17,18]. These phenomena can occur during population expansion processes. While mate-choice copying did affect the rate at which a population adapts to a new environment, as predicted, the effects and the role of copying in population range expansion, were different from what we originally predicted. Our results show some unexpected consequences and emergent properties that can arise at the population level when considering the role of mate-choice copying. They also suggest that different mate-choice copying types, preference rules, and female choosiness may lead to different ecological and evolutionary consequences to be considered in future research.

Case 1: Preference is condition independent

To understand the numerical results, one should appreciate the specific differences governing the different types of mate-choice copying and preference rules. Starting from the no copying condition (the 'null' situation), we observe that the frequency of the dispersal allele remains around its initial value of 0.02 and, because of the migration load, it takes more than 1,000 generations (2,500 with fixed migration) to breach the environment when females are choosy. Individual copying worsens the situation, because in this case, despite the substantial increase in dispersal, it can take as much or more time to breach the environment. It is clear that individual copying is a highly maladaptive strategy and the frequency of the copying allele decreases sharply, resulting in a preference mismatch similar to that of no copying. Generalized copying increases both the speed taken for the population to breach the environmental gradient, and the frequency of the copying allele during the invasion of novel environments. This happens notwithstanding the higher mismatch between female preference and the average environmental value (Figure 1F).

Generalized copying breached the environmental gradient faster than individual copying or populations with no copying behaviour. This happens because in generalized copying we considered that copier females will still need decide which male is "similar enough" to the one they observed. By introducing this additional source of variation, and given that non-copier females has a high mismatch with the optimal trait in the patches, generalized copying would actually reframe the preference of copier females, and the additional source of variation would allow for some (but not all) of the copier females to effectively choose more adapted males. In individual copying, by choosing the "most popular" male, females do not deviate from the male phenotype chosen by non-copier females and because these males are not well adapted to the new patches, these females will produce less adapted offspring.

Note that when dispersal was not allowed to evolve, we also eliminated individual variation in dispersal and, thus, there is no 'spatial sorting' of high-dispersal individuals during the invasion period that could accelerate the time to breach [34,35]. This result contrasts with that of Sapage et al. [18], where the authors found higher dispersal with generalization. The discrepancy is likely due to the fact that in our present scenario the

379 initial habitat grid has a small random noise that is independent on distance. Overall, the

380 results suggest that with generalized copying there is a positive frequency-dependent

381 advantage for the more common male trait allele, leading to a coevolution between the

382 trait allele and the copying allele.

383 A puzzling question is why dispersal ability increases with individual copying but

384 not with generalized copying, a result that is largely independent of the intensity of sexual

385 selection (Figure 1B). This pattern of dispersal is established after the warmup period and

386 before expansion and influences the behaviour of the populations during expansion as

387 well. We think that this happens with individual copying because if many females choose

388 the same male, many offspring in the same patch will not only share the same trait, but

389 also the same dispersal ability. Over time, offspring with lower dispersal ability will

390 mostly compete among themselves, while offspring with higher dispersal ability will

391 mostly compete with others, making high dispersal more adaptive. This does not happen

392 with generalized copying because low or high dispersal is likely to lead individuals to

393 similar competitive environments.

394 During the invasion period, a higher dispersal ability may also mitigate some of

395 the maladaptive effects that limit population spread [36–39]. With individual copying,

396 many copier females will choose the exact same male, which can also be maladaptive

397 because the most popular male is not necessarily the best male in the new patch (since

398 viability selection happens before individuals disperse). In addition, if the frequency of

399 copiers choosing the same male is high, dispersal would reduce the genetic variation at

400 the edge of expansion, which would also hinder local adaptation. In this case, females

401 would be better off not copying at all. This is probably the reason why it takes longer for

402 populations with individual copying to breach the environmental gradient when dispersal

403 is fixed and choosiness is high (Figure 1C), and why the frequency of the choosing allele

404 drops significantly before and during the invasion with individual copying (Figures 1D

405 and 1E).

406 Another important point to note is that we assumed that females had perfect

407 information about all the non-copiers' matings in a patch. Eavesdropping is an important

408 component of mate-choice copying [13,40], and the ability of females to observe other

409 matings should depend on many different factors. Reducing the number of matings

410 observed by females should increase the number of different males chosen by copiers

411 within each patch, thus making individual copying more like generalized copying.
412 However, this remains to be tested and is difficult to implement, as individual
413 subsampling would increase the computational time to an unacceptable level.

414   To sum up, when preference is condition independent, generalized copying might
415 serve as a shortcut for eventual adaptation to new environments, with individuals
416 ultimately aligning their innate preference towards the best adapted individuals in the
417 long run. Indeed, given the relatively high level of environmental selection, individuals
418 can only advance in the environmental gradient if their trait allele closely matches the
419 environmental value; (see Figure S2). However, this does not prevent generalized
420 copying from increasing the rate of expansion, making this type of social learning a non-
421 negligible mechanism for the ecology and evolution of populations. Therefore, with
422 generalized copying, we show that range expansion can occur and be accelerated even
423 without the effect of cultural evolution – through oblique or vertical transmission of social
424 information [4,23] –, which we did not include in our model.

425

Case 2: Preference is condition dependent

427   When female preference is condition independent, females are selected to prefer
428 males with traits adapted to their original environment, so natural selection opposes
429 sexual selection as individuals expand into a new patch. However, when female
430 preference is towards a male trait that is condition dependent, sexual selection no longer
431 opposes natural selection during population expansion and populations breach the
432 environment faster in all cases (c.f. Figures 1A and 2A). This faster breach also occurs
433 when individual variation in dispersal has been eliminated, especially for high choosiness
434 (c.f. Figures 1C and 2C). As observed in case 1, individual copying again increases
435 dispersal more and decreases the proportion of individuals with the copying allele more
436 than generalized copying. However, in contrast to case 1, individual copying is now the
437 best mating strategy to drive the population to a faster breach.

438   The increase in dispersal ability with individual copying may be due, as explained
439 for case 1, to the fact that many offspring in the same patch share not only the same trait,
440 but also the same dispersal ability, with higher dispersal reducing competition between
441 siblings and thus being more adaptive (Figures 1B and 2B). However, when preference

442 is condition dependent, fixing dispersal reduces the performance of both individual and
443 generalized mate-choice copying (Figure 2C). Thus, the effect that we observe on
444 expansion rate is not only due to copying behaviour but also to dispersal.

445   Also, when preference is condition dependent, the copying allele for individual
446 copying remains on average below 0.5, which is the expected mutational equilibrium
447 value (Figure 2D and 2E). This selection against the copying allele (as found previously
448 [10]) suggests that there is a slight trade-off between MCC and dispersal. Furthermore,
449 non-copier females already have perfect information about male quality, so the copying
450 allele can never outperform the non-copying allele. This disadvantage is even stronger
451 for generalised copying, where females tend to choose less adapted males, by choosing a
452 "similar enough" male, whereas in individual copying females tend to choose more
453 adapted males by choosing the "most popular" male. This causes the copying allele of
454 populations with generalized copying to decrease at the expansion front when choosiness
455 is high, and even more so than in populations with individual copying, in contrast to what
456 happens when preference is condition independent (c.f. Figures 1E and 2E). Thus, when
457 the preference is condition dependent, a population with generalized copying no longer
458 performs better than populations with individual copying or populations with no copying
459 behaviour.

460   Overall, our results highlight the importance of considering the interaction
461 between female preference and the type of mate-choice copying rule. When preference is
462 condition-independent, generalized copying helps populations to adapt more quickly to
463 the environmental gradient, but when preference is condition dependent it is individual
464 copying that is more advantageous, although some selection against the copying allele is
465 also observed in these circumstances. This means that mate-choice copying can speed up
466 the expansion process, but the conditions under which it can do so depend on many other
467 factors.

468

General remarks

470   There is a lack of empirical studies exploring the effects of mate-choice copying
471 on population dynamics, with only a few studies comparing differences in copying
472 behaviour between different populations [41,42]. We acknowledge that it is difficult to

473 test these effects empirically, but we urge empiricists to at least experiment with which
474 set of rules prevails in the species they study, particularly with regard to the assumptions
475 of the current model, namely the type of mate-choice copying and preference rules used
476 by females.

477   Some empirical research has already shown in two model species, that females
478 can copy individuals or generalize what they have learned, or that they can copy
479 condition-dependent and condition-independent traits. This is the case in female fruit flies
480 *Drosophila melanogaster*, which can change their preference for individual males of large
481 or small size, a condition-dependent phenotype generated by exposing young individuals
482 to different growth conditions [43]. In addition, fruit flies are also able to generalize males
483 powdered with different colours, a trait that is independent of male condition [43].
484 Generalized copying of condition-independent traits has also been found in the guppy
485 *Poecilia reticulata*, where females generalize male colour patterns [44], a trait that has
486 high heritability [25]. Alternatively, females might also decide not to copy if they perceive
487 one male to be ostensibly more attractive than another [45,46,47]. The next step would
488 be to investigate which of these scenarios are more likely to occur in the wild, and under
489 what conditions. For example, it would be interesting to understand if and how an
490 individual copies the mate choice of others when they are exposed to a familiar *versus*
491 unfamiliar environments, or when exposed to familiar *versus* unfamiliar demonstrators.
492 These scenarios can simulate different dispersal patterns that a population might
493 encounter, and the results can help build more accurate models to predict the effects of
494 mate-choice copying. When considering which traits to copy, a recent article suggests a
495 generalized mechanism for sexual selection that involves social learning, called "the
496 inferred attractiveness hypothesis" [48]. This hypothesis suggests that social learning in
497 mate-choice is dynamic, and females tend to generalize the trait of the target male that is
498 less common in a population. This mechanism can lead to variation in traits and
499 preferences, and it would be interesting to use this framework to model the effects of
500 mate-choice copying in population expansion in the future.

501   Another important assumption of the current model is how we defined the
502 conformity rules for the two types of mate-choice copying we tested. Conformity to the
503 majority rule is considered an important feature in the cognitive process underlying social
504 learning, as it allows for the maintenance of the cultural information being transmitted
505 [17,49]. It can be present in both individual and generalized copying. In the first case, it

concerns the most popular male and in the second the most popular phenotype. Thus, when we simulated individual copying, we thus had the copying females in each patch choose the locally most popular male, whereas when we simulated generalized copying we had the copying females in each patch choose males with the locally most popular phenotype. The difference between the two types of conformity rules is that individual copying is more deterministic because females have only one male to choose from, while in generalized copying they can choose between several similar males. On the other hand, the similarity between the two types of conformity rules is that females observe multiple matings in both cases. In our model, we extrapolate this rule to its maximum, by assuming that copying females can observe all matings of non-copying females in their patch. Of course, one can argue that females can only observe or process a limited number of matings due to temporal, ecological, or cognitive constraints, leading to sampling differences between females. In individual copying, the most popular male may also not be available, forcing females to choose other, similar males. These limitations increase the differences between what each female has learned, making the consequences of copying for population dynamics perhaps more stochastic and, therefore more difficult to predict. These limitations also dilute the differences between the two types of copying, making their mathematical modelling as distinct behaviours perhaps unrealistic. Given that unavailability of the most popular male is likely to be common in nature, particularly in monogamous species, generalized copying is likely to be more common. However, only empirical studies can tell us how common each type of copying is in nature, and only neuroethological studies of the cognitive mechanisms underlying each type of copying can tell us about whether or not they are actually different mechanisms.

In our model, we also assumed for simplicity that dispersal and copying are determined by single alleles, but could be affected by additional conditions that we did not model. For example, dispersal is known to be influenced by sex [50], personality [51], or population density [52], while mate-choice copying can be influenced by the age [53] or quality [54] of the demonstrators. These types of conditioning factors would again increase the differences between what each female learns, or how, or when, making models more complex but also more realistic. Therefore, in our current study, we have only scratched the surface of the true effects of mate-choice copying on population dynamics, but we consider it an important first step, focusing on population range

538 expansion, while warning for different potential outcomes depending on the broad
539 copying types and preference rules that have already been shown to exist.

540   Species distribution range is one of the core questions in ecology and evolution,
541 and extensive studies have been conducted to understand how populations disperse and
542 adapt to new environments [e.g., 55]. On the other hand, only a few studies have shown
543 that social information can influence individuals' dispersal decisions [e.g., 56], and in
544 particular mate-choice copying can be beneficial for dispersal because it can aid adaption
545 to a new environment by promoting copying of the local individuals' mate choices [18].
546 However, the effects of mate-choice copying in an expanding population have never been
547 investigated. Although we have not exhausted the parameter space of our model and have
548 not explored every possible effect of copying, our study already shows that mate-choice
549 copying, a social learning behaviour, can accelerate a species range expansion in a
550 scenario where the new habitat is empty. It would now be interesting to model a different
551 set of parameters in a scenario where the new habitat is not empty. Due to the current
552 anthropogenic acceleration of environmental change, many species face the challenge of
553 adapting to new conditions or changing their habitat range [57]. They will only rarely find
554 empty habitats, so it is important to understand whether social learning through mate-
555 choice copying can still facilitate adaptation in the face of competition from the resident,
556 more adapted population. Based on our previous [18] and current theoretical studies, we
557 predict that if migrant females copy the choices of local females, the adaptation process
558 will be facilitated, unless the genetic distance between the migrant and the resident
559 populations is too large, in which case mate-choice copying could be maladaptive. Mate-
560 choice copying has been hypothesised to promote hybridisation between conspecific and
561 heterospecific populations, but its fitness consequences, whether positive or negative, will
562 depend on the characteristics of the populations under study [17].

563   Mate-choice copying was initially suspected in lekking bird species [2], but this
564 behaviour is now known to be widespread in nature [58]. Recently, the effects of this
565 behaviour have been theorized in population ecology and evolution [17], but it has been
566 difficult to study their effects using only empirical studies. Empirical, and theoretical
567 studies need to work in tandem to advance this field, and this task needs to be undertaken
568 not only by behavioural ecologists but also by a multidisciplinary network also including
569 ecologists, evolutionary biologists, neuroethologists, and mathematicians. This area is
570 important in the context of global environmental change, where the combined effects of

social learning and sexual selection in shaping adaptation could be a promising new avenue of research.

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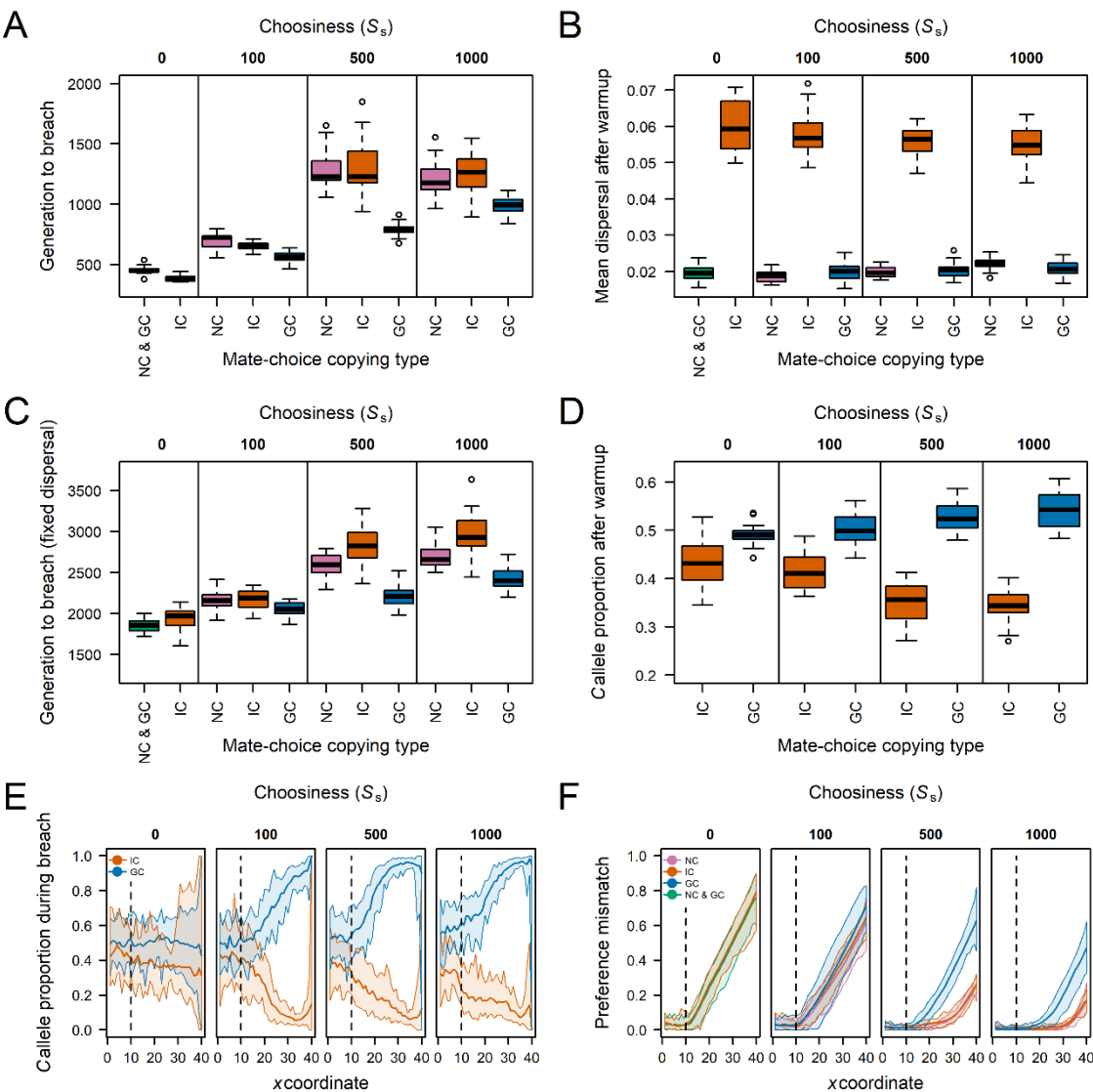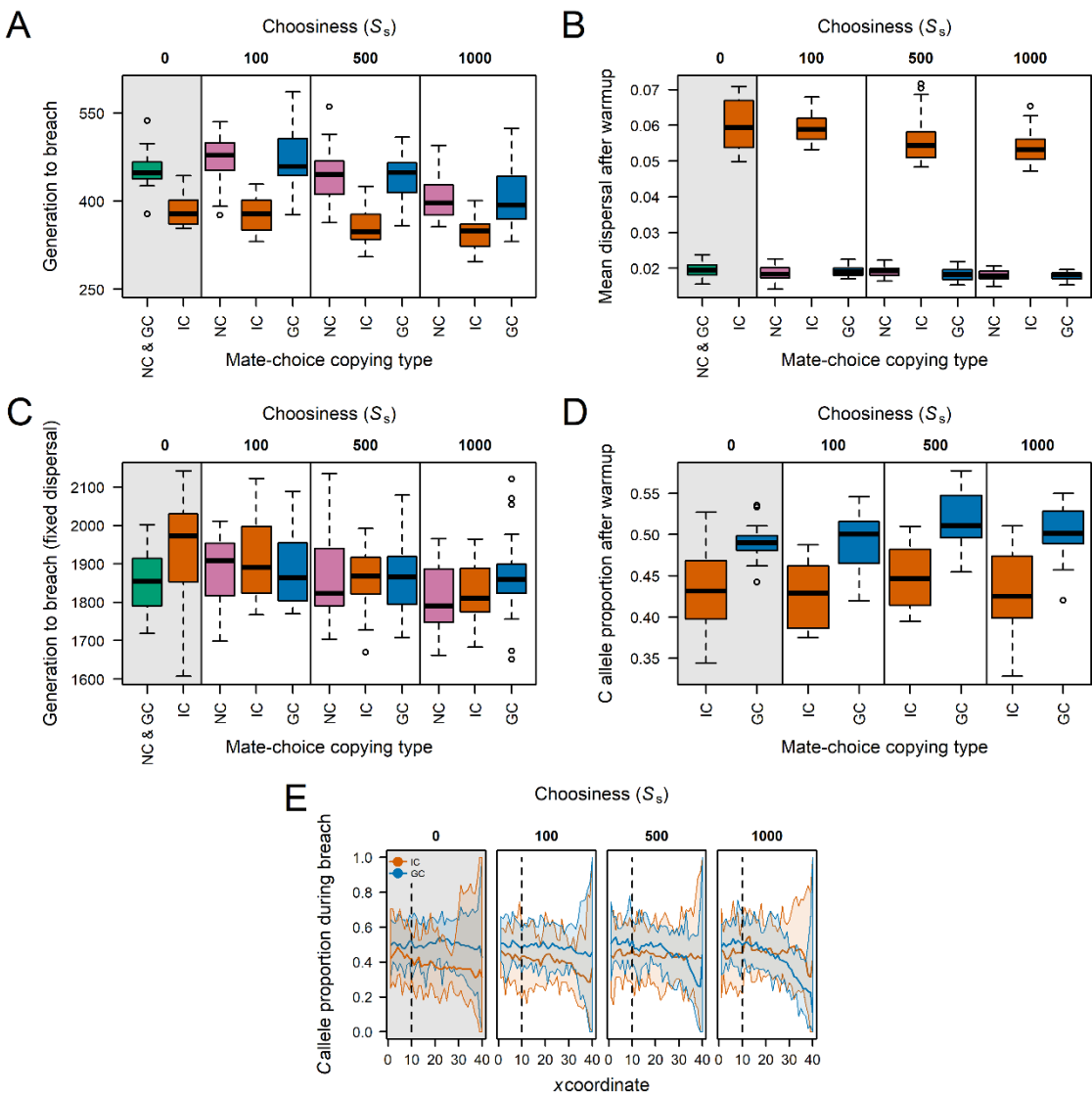# Tables and Figures

Figure 1

Figure 1: Results of simulations where preference is for condition independent male traits. Except for panel C, all panels show results from simulations where dispersal is allowed to evolve. Panels A and C show the number of generations taken to breach the environmental gradient after warmup when dispersal is evolving or fixed, respectively. Panels B and D show, respectively, the mean dispersal allele value and the C allele proportion after warmup but before expansion. Panel E shows the C allele proportion per column during the generation where the population breaches the environmental gradient. Panel F shows the difference between the mean preference allele and the average environmental value within each column during the same generation as Panel E. The dashed line in Panels E and F indicate the separation between the initial habitat on the left and the environmental gradient on the right. In panels A–D, the thick line in each box plot represents the median value of 20 replicates, and the lower and upper margins of the box indicate the 25% and 75% interquartile range. Vertical dashed lines show extreme values within 1.5 times the interquartile range, while values outside this range are represented by open circles. NC = No copying; IC = Individual copying; GC = Generalized copying.

Figure 2

769 **Figure 2: Results of simulations where preference is for condition dependent male**

770 **traits**. Panels follow the same description as in Figure 1. Results with $S_S = 0$ (light grey

771 background) are taken from the same simulations as in Figure 1 as they are equivalent

772 for both simulations, and they are plotted comparison purposes.